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Reevaluation of the hermit crab genus *Parapagurodes* McLaughlin & Haig, 1973 (Decapoda: Anomura: Paguroidea: Paguridae) and a new genus for *Parapagurodes doederleini* (Doflein, 1902)

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Abstract.—The question of polyphyly in the hermit crab genus, *Parapagurodes* McLaughlin & Haig, 1973, has been investigated by comparisons of a series of morphological characters among the eight species presently assigned to the genus. The results of the analysis have shown that the only mutually shared characters are an acutely developed rostrum and the presence, in males, of a short or very short right sexual tube. Consequently, the composition of *Parapagurodes* is herein restricted to the two species originally assigned, viz. *P. makarovi* McLaughlin & Haig, 1973, and *P. laurentae* McLaughlin & Haig, 1973. *Parapagurodes hartae* McLaughlin & Jensen, 1996, is transferred to the genus *Pagurus,* and four species subsequently transferred from *Pagurus* to *Parapagurodes,* viz. *P. gracilipes* (Stimpson, 1858), *P. nipponensis* (Yokoya, 1933), *P. constans* (Stimpson, 1858), and *P. imaii* (Yokoya, 1939) are returned to *Pagurus.* A new genus, *Dofleinia,* is proposed for the species, *Parapagurodes doederleini* (Doflein).

When first proposed, the genus *Parapagurodes* McLaughlin & Haig, 1973, was characterized, in part, as having 11 pairs of biserial gills; a moderately well developed, but not recurved external lobe of the maxillulary endopod; fifth pereopods with coxae symmetrical; males with a short right sexual tube, and biramous left pleopods absent or weakly developed on pleomeres (cf. Schram & Koenmann 2003) 3–5; females lacking paired first pleopods, with biramous left pleopods 2–4 weakly to moderately well developed, left fifth pleopod weakly developed or absent; and a telson with terminal margins straight, slightly concave or slightly oblique. Additionally, the authors noted that while a right sexual tube was always present in mature males, its length and orientation were variable, and in one specimen both right and left tubes were present. Variations also were observed in the number and development of male and female pleopods in both *P. makarovi* McLaughlin & Haig, 1973, the type species of the genus, and the second described species, *P. laurentae* McLaughlin & Haig, 1973. In recent years, one new species, *P. hartae* McLaughlin & Jensen, 1996, has been described in the genus, and five Japanese species have been transferred to it viz.: *Pagurus gracilipes* (Stimpson, 1858), *P. nipponensis* (Yokoya, 1933), *P. constans* (Stimpson, 1858), and *P. imaii* (Yokoya, 1939) by Komai (1998, 1999) and *Catapagurus doederleini* Doflein, 1902 by Asakura (2001).

At the time of the establishment of *Parapagurodes* McLaughlin & Haig, 1973, male sexual tube development had been reported in less than two dozen genera. McLaughlin & Haig (1973) could relate *Parapagurodes* to only two of those genera,

Pagurodes Henderson, 1888 and *Acanthopagurus* de Saint Laurent, 1969, but cited several characters by which the three genera could be separated. In the subsequent 30 years the number of genera with documented sexual tube development has more than doubled (cf. McLaughlin 2003). Nonetheless, *Parapagurodes* still can be allied only to *Pagurodes* and *Acanthopagurus* and more remotely to *Catapagurus* A. Milne Edwards, 1880. However, recently the monophyly of *Parapagurodes* itself has come under question (Lemaitre & McLaughlin 2003b).

In their introductory remarks regarding *Parapagurodes hartae,* McLaughlin & Jensen (1996: 841) made the unfortunate statement that "... males have a small sexual tube on the coxa of the right fifth pereopod. This species, therefore, cannot be attributed to *Pagurus,* but must be assigned to *Parapagurodes* . . ." The comment was prompted by the fact that prior to their description of *P. hartae,* this taxon had been reported from California and Washington, USA, and British Columbia, Canada, as *Pagurus* sp. (McLaughlin & Haig 1973, Hart 1982, Jensen 1995). Regrettably, McLaughlin & Jensen's (1996) remark has been interpreted by some carcinologists to mean that species with papillae and/or very short sexual tubes are automatically excluded from the genus *Pagurus* (e.g., Komai 1998, 1999). According to the views of McLaughlin & Lemaitre (2001) and Lemaitre & McLaughlin (2003a, 2003b), the presence or absence of very short male sexual tubes and/or papillae should not be seen as the single cause to transfer species from genera to which they are otherwise morphologically attributable, or assign species to genera that they are not otherwise morphologically allied.

McLaughlin & Jensen (1996) justified their generic assignment on the basis of morphological and larval similarities among the three species then assigned to *Parapagurodes.* However, they also pointed out, as McLaughlin & Haig (1973) had for *P. laurentae,* that *P. hartae* had superficial resemblances to a few northeastern Pacific species of *Pagurus.*

Upon the observation of very short sexual tubes in *Pagurus gracilipes* and *P. nipponensis,* Komai (1998) provisionally transferred these two species to *Parapagurodes,* while noting their close similarities to species of McLaughlin's (1974) *bernhardus* group of *Pagurus.* Komai (1998) also pointed out that while *Pagurus gracilipes* and *P. nipponensis* shared the presence of a small right male sexual tube, both species differed substantially from *Parapagurodes makarovi, P. laurentae,* and *P. hartae.*

In the subsequent, continuing study of Japanese species of *Pagurus,* Komai (1999) transferred *Pagurus constans* and *P. imaii* to *Parapagurodes* because he found very short male sexual tubes on both fifth coxae in the former species, and a single right tube in the latter. He also provided a minor emendation to the generic diagnosis by calling attention to the slight median indentation, cleft or concavity sometimes seen in the gill lamellae, and to the occurrence of the left sexual tube, although he acknowledged that McLaughlin & Haig (1973) similarly had reported the rare occurrence of a left tube in *P. makarovi.* Unfortunately, Komai's (1999) emendation, like McLaughlin & Jensen's (1996) brief generic diagnosis, failed to acknowledge the absence or reduction in number of male pleopods and the usual absence of the fifth left female pleopod in the type species.

In his review of the genus *Catapagurus* A. Milne-Edwards, 1880, Asakura (2001) redescribed *Catapagurus doederleini* and found it to be markedly divergent from all other species that had been assigned to *Catapagurus.* Asakura transferred Doflein's (1902) taxon to *Parapagurodes* stating that it agreed with all the diagnostic characters proposed by McLaughlin & Haig (1973) for their genus; however, it was primarily the presence of a very short right sexual tube that prompted his action. He quite correctly acknowledged the dimorphic second pereopods of *P. doederleini,* as well as the lack

of corneous spines on the ventral margins of the second right and both third pereopods.

As previously indicated, Lemaitre & McLaughlin (2003b) expressed the opinion that *Parapagurodes,* as presently constituted, represented a polyphyletic taxon. To evaluate the merits of their conclusion, we have critically reviewed the descriptions of each of the assigned taxa. We have supplemented these reviews by reexamining specimens of *Parapagurodes laurentae* and *P. hartae* in the first author's personal collections (PMcL). Additionally we have examined representatives of *P. constans, P. doederleini, P. gracilipes, P. imaii,* and *P. nipponensis* from the collections of the Natural History Museum and Institute, Chiba (CBM-ZC), the Hilgendorf collection from the Museum für Naturkunde, Berlin, Germany (ZMB), and specimens donated to one of the authors by Dr. M. Imafuku, Kyoto University. From our reviews and examinations, we present the comparative diagnoses of the eight species we have used to determine the validity of the current generic assignments.

Animal size is indicated by shield length (sl) as measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. Reported sexual tube length corresponds to the criterion of McLaughlin (2003): very short (<1 coxal length), short (1–2 coxal lengths), moderate (>2–5 coxal lengths). The reference by McLaughlin & Haig (1973) to the fourth pereopod being subchelate or not subchelate is interpreted here according to McLaughlin (1997) who recognized three conditions in the propodal-dactyl articulation of this appendage. McLaughlin & Haig's (1973) "subchelate" is viewed by McLaughlin (1997) as being semichelate, whereas McLaughlin & Haig's (1973) "not subchelate" is now considered to actually be subchelate. The abbreviation ovig. indicates ovigerous female. Previously published illustrations used in this manuscript are of specimens in the collections of the Los Angeles Country Natural History Museum (LACM) [transferred to that Museum from the Allan Hancock Foundation (AHF)], Los Angeles, California; the Royal British Columbia Provincial Museum (RBCPM), Victoria, British Columbia; and Zoologische Staatssammlung München (ZSSM), Munich.

Review and Reexamination

Parapagurodes makarovi McLaughlin & Haig, 1973

Figs. 1A, 2A, 3A, 4A, B, 5A

Description by McLaughlin & Haig (1973:119–120, figs. 4a, 5–8). No supplemental material available.

Diagnosis.—Gill lamellae essentially biserial but with or without very weak distal indentation or concavity. Rostrum acutely triangular. Maxillule with somewhat produced endopodal external lobe, not recurved. Right cheliped elongate, more so in large individuals; dorsal surface of palm distinctly convex; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped elongate dorsal surface of palm convex, elevated in midline proximally. Ambulatory legs similar, somewhat laterally compressed; dactyls as long or longer than propodi, slender, in dorsal view straight, each with row of corneous spines on ventral margin; carpi each with dorsodistal spine. Fourth pereopods usually subchelate, occasionally weakly semichelate; preungual process very small; propodal rasp with 1–3 irregular rows of corneous scales. Sternite of third pereopods (sixth thoracomere) semi- or subsemicircular. Sternite of fifth pereopods (eighth thoracomere) separated into two broad lobes by weak median depression; coxae of fifth pereopods symmetrical. Males with short sexual tube developed from coxa of right fifth pereopod; left gonopore sometimes with papilla, occasionally with short tube. No paired pleopods in either sex. Males usually without, occasionally with weakly biramous left pleopods on pleomeres 3 and 4. Females with weakly developed, biramous left

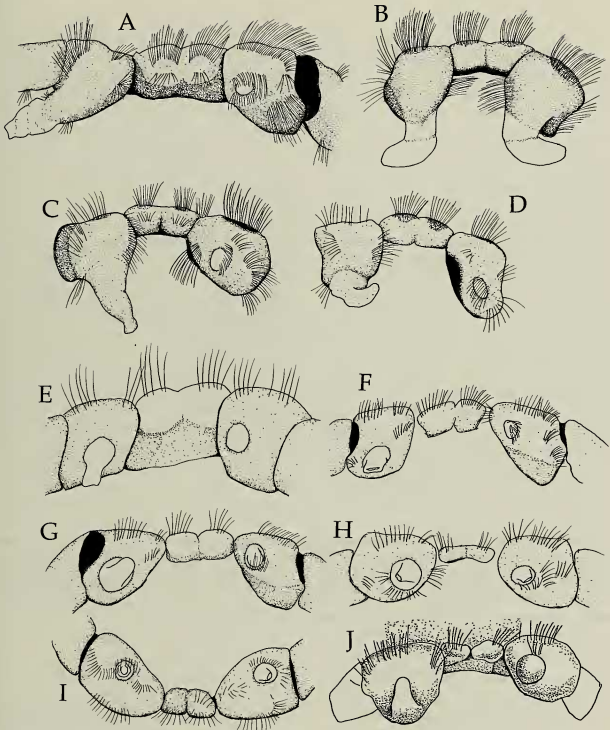


Fig. 1. Coxae and sternite of fifth pereopods. A, B, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), ♂ (sl = 3.6 mm), LACM; C, D, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), ♂ (sl = 3.4 mm), LACM; E, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; F, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; G, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; H, *P. constans* (Stimpson, 1858), ♂ (sl = 8.7 mm), CBM-ZC 59; I, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; J, *P. doederleini* (*Doflein, 1902*), ♂ (sl = 8.6 mm), ZSSM 274/1. A–D redrawn from McLaughlin & Haig (1973); E redrawn from McLaughlin & Jensen (1996); J from Asakura (2001).

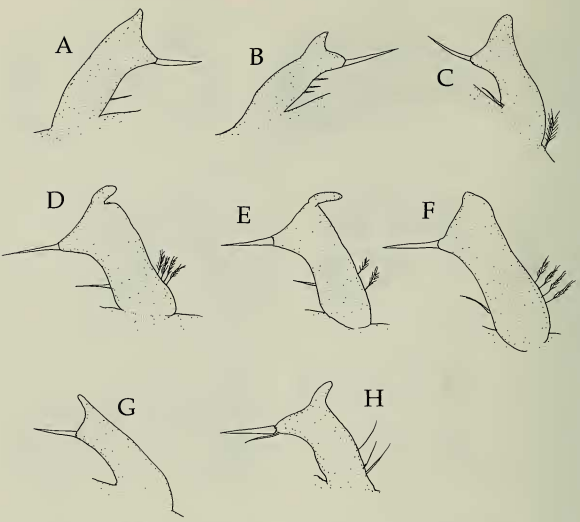


Fig. 2. Endopod of maxillule. A, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, *P. constans* (Stimpson, 1858); ♂ (sl = 8.7 mm), CBM-ZC 59; G, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; H, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); H from Asakura (2001).

pleopods on pleomeres 2–4, pleopod 5 absent or rudimentary. Telson with posterior lobes separated by very small, shallow median cleft; terminal margins straight or somewhat concave, each with several to numerous spinules or small to very small spines.

Parapagurodes laurentae McLaughlin & Haig, 1973
Figs. 1B, 2B, 3B, 4C, D, 5B

Description by McLaughlin & Haig (1973:129–134, figs. 4b, 9–11).

Supplemental material examined.—U.S.A.: 3 ♂ (sl = 1.4–2.9 mm), 3 ♀ (sl = 1.7–2.9 mm), 2.5 mi SE Seal Rocks, Santa Catalina I, CA, 159–174 m, 25 Oct 1941, PMcL.

Diagnosis.—Gill lamellae essentially biserial but with or without very weak distal indentation or concavity. Rostrum acutely triangular. Maxillule with moderately well developed endopodal external lobe, not recurved. Right cheliped usually elongate, more so in large individuals; dorsal surface of palm convex; dorsal surface of

carpus with row of spines mesiad of midline. Left cheliped moderately long, dorsal surface of palm convex. Ambulatory legs similar, somewhat laterally compressed, dactyls as long or longer than propodi, slender, in dorsal view usually straight, with row of corneous spines on ventral margin; carpi each with dorsodistal spine. Fourth pereopods usually semichelate, occasionally subchelate; preungual process very small; propodal rasp with 1–3 irregular rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subsemicircular. Sternite of fifth pereopods (eighth thoracomere) separated into two broad lobes by weak to moderate median depression; coxae of fifth pereopods symmetrical. Males with short or very short sexual tube developed from coxa of right fifth pereopod; left gonopore sometimes with papilla. No paired pleopods in either sex. Males usually with weakly biramous left pleopods on pleomeres 3 and 4, occasionally without unpaired pleopods. Females usually with moderately well developed, biramous pleopods on pleomere 2–4; pleopod 5 rudimentary, rarely absent. Telson with posterior lobes separated by very shallow median cleft; terminal margins concave or slightly oblique, each with row of very small spinules and 1–4 small spines at posterolateral angles.

Parapagurodes hartae McLaughlin & Jensen, 1996
Figs. 1C, 2C, 3C, 4E, 5C

Description by McLaughlin & Jensen (1996:844–847, figs. 1–4).

Supplemental material examined.—Canada: 1 ♂ (sl = 1.1 mm), 1 ♀ (sl = 1.5 mm), Taylor Inlet, Barkley Sound, British Columbia, 10 m, 10 Jun 1994, PMcL.

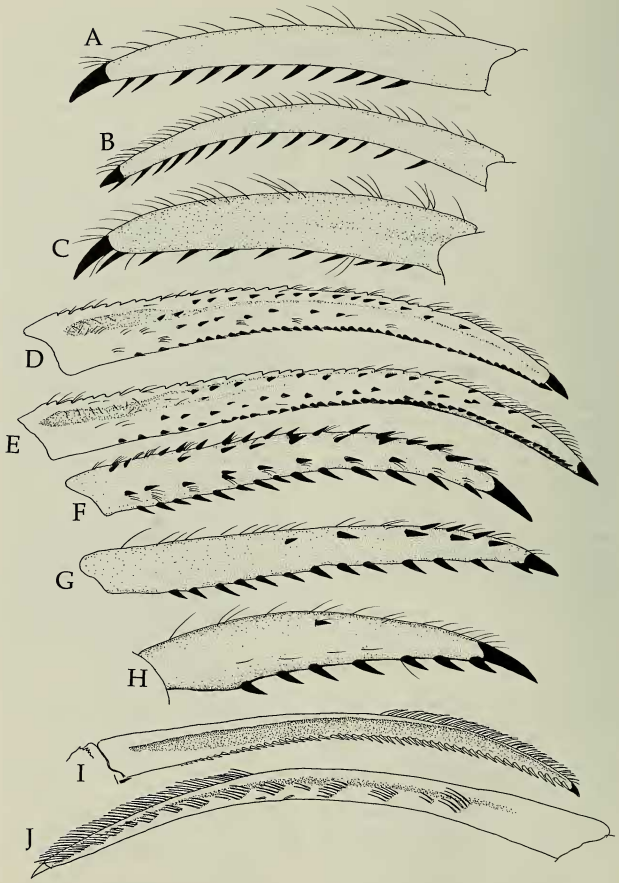
Diagnosis.—Gill lamellae essentially biserial but with or without very weak distal indentation or concavity. Rostrum acutely triangular. Maxillule with moderately well developed endopodal external lobe, not recurved. Right cheliped elongate in large males; dorsal surface of palm convex; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped with dactyl and fixed finger short and broad in small males and females, longer in large males; dorsal surface of palm convex. Ambulatory legs similar; dactyls slightly shorter to slightly longer than propodi, moderately slender, laterally compressed, in dorsal view straight, with row of corneous spines on ventral margin; carpi each with dorsodistal spine and row of low, sometimes spinulose protuberances on dorsal surface, rarely 1 dorsoproximal spines (second pereopods). Fourth pereopods usually semichelate, occasionally subchelate; preungual process very small; propodal rasp with 2–4 irregular rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subsemicircular to subrectangular. Sternite of fifth pereopods (eighth thoracomere) separated into two broad lobes by weak to moderate median depression; coxae of fifth pereopods symmetrical. Males often with very short sexual tube developed from coxa of right fifth pereopod; left gonopore without papilla. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, left biramous pleopods on pleomeres 2–4; pleopod 5 as in male. Telson with posterior lobes separated by shallow, U-shaped median cleft; terminal margins rounded or slightly oblique, each with row of very small spinules and 1or 2 small spines at posterolateral angles.

Parapagurodes gracilipes (Stimpson, 1858)
Figs. 1D, 2D, 3D, 4F, 5D

Redescription by Komai (1998:268–275, figs. 1A, 2–5, 7).

Supplemental material examined.—Japan: 2 ♂ (sl = 5.4, 9.0 mm), 1 ♀ (sl = 6.7 mm), off Choshi, Chiba, 10–20 m, 3 Sep 1996, CBM-ZC 2977.

Diagnosis.—Gill lamellae biserial. Rostrum acutely triangular. Maxillule with


A
B
C
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somewhat produced endopodal external lobe, slightly to distinctly recurved. Right cheliped moderately (small specimens) to considerably elongate in large individuals; dorsal surface of palm weakly convex but with dorsomesial portion somewhat elevated; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped with dorsal surface of palm somewhat flattened, dorsomesial and dorsolateral margins slightly elevated. Ambulatory legs similar; dactyls longer than propodi, strongly twisted; moderately broad, each with row of numerous corneous spines on ventral margin; carpi each with single or double row of multifid spines. Fourth pereopods semichelate; no preungual process; propodal rasp with several rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subquadrate, weakly skewed, sulcate medially. Sternite of fifth pereopods (eighth thoracomere) separated into two subovate lobes by shallow median groove; coxae of fifth pereopods symmetrical. Males with very short sexual tube developed from coxa of right fifth pereopod; left gonopore without tube or papilla. No paired pleopods in either sex. Males with unequally biramous pleopods on pleomeres 3–5. Females with well developed, biramous pleopods on pleomeres 2–4; pleopod 5 with endopod noticeably reduced. Telson with posterior lobes separated by very small, or indistinct median cleft; terminal margins nearly horizontal, each with eight to ten small spines and two or three larger spines at posterolateral angles, lateral margins occasionally with spinules.

Parapagurodes nipponensis (Yokoya, 1933)
Figs. 1E, 2E, 3E, 4G, 5E

Redescribed by Komai (1998:275–279, figs 1B, 6, 7) only as similar to *P. gracilipes* with certain noted differences.

Supplemental material examined.—Japan: 4 ♂ (sl = 6.3–7.6 mm), 1 ♀ (sl = 5.3 mm), Kumano Nada, 50 m, Sep 1981, PMcL; 2 ♂ (sl = 8.0, 9.2 mm), off Kashima, Irakaki, 65 m, 24 Apr 1991, CBM-ZC 50; 1 ♂ (sl = 7.3 mm), off Kii Minabe, Kii Peninsula, 80–100 M, 24 Mar 1995, CBM-ZC 1162.

Diagnosis.—Gill lamellae biserial. Rostrum acutely triangular. Maxillule with somewhat produced external lobe, slightly to distinctly recurved. Right cheliped moderately (small specimens) to considerably elongate in large individuals; dorsal surface of palm weakly convex but with dorsomesial marginal area somewhat elevated; dorsal surface of carpus with row of spines mesiad of midline. Left cheliped with dorsal surface of palm somewhat flattened, dorsomesial and dorsolateral margins slightly elevated. Ambulatory legs similar; dactyls longer than propodi, strongly twisted; moderately slender to moderately broad; each with prominent longitudinal sulcus on lateral face and row of numerous very tiny corneous spines on ventral margin; carpi each with single or double row of multifid spines. Fourth pereopods semichelate; no preungual process; propodal rasp with several rows of corneous scales. Sternite of third pereopods (sixth thoracomere) sub-

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Fig. 3. Ambulatory dactyls. A–H, dactyl of left third pereopod (A–C lateral view, D–H, mesial view); I, dactyl of left second pereopod (mesial view); J, dactyl of right second pereopod (mesial view). A, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.2 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 2.8 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, *P. constans* (Stimpson, 1858), ♂ (sl = 8.7 mm), CBM-ZC 59; G, H, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699, ovig. ♀ (sl = 1.6 mm), CBM-ZC 1911; I, J, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); I, J from Asakura (2001).

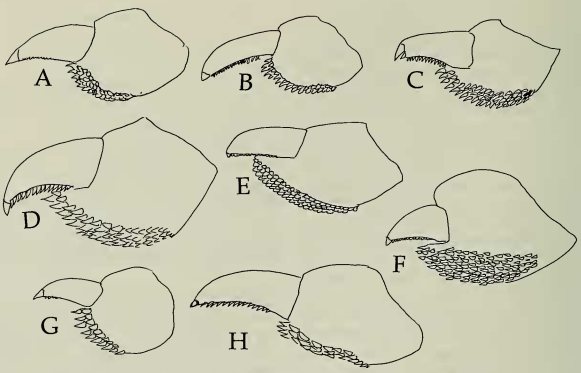

Fig. 4. Dactyl and propodus of left fourth pereopod (lateral view). A, *Parapagurodes makarovi* McLaughlin & Haig, 1973, ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, *P. constans* (Stimpson, 1858), ♂ (sl = 8.7 mm), CBM-ZC 59; G, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; H, *P. doederleini* (*Doflein, 1902*), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); H redrawn from Asakura (2001).

quadrate to subrectangular. Sternite of fifth pereopods (eighth thoracomere) separated into two subovate lobes by shallow median groove; coxae of fifth pereopods symmetrical. Males with very short sexual tube developed from coxa of right fifth pereopod; left gonopore without tube or papilla. No paired pleopods in either sex. Males with unequally biramous pleopods on pleomeres 3–5. Females with well developed, biramous pleopods on pleomeres 2–4; pleopod 5 with endopod noticeably reduced. Telson with posterior lobes separated by very small median cleft; terminal margins oblique, each with 8 or 9 small spines and 1 larger spine at posterolateral angles.

Parapagurodes constans (Stimpson, 1858)
Figs. 1F, 2F, 3F, 4H, 5F, G

Redescription by Komai (1999:80–88, figs. 1–4).

Supplemental material examined.—Japan: Hilgendorf collection, 1 ovig. ♀ (sl = 5.5 mm), ZMB 8650; 1 ♂ (sl = 11.1 mm), 1 ovig. ♀ (sl = 10.2 mm), Sagami Bay, ZMB 17800; 1 ♂ (sl = 8.7 mm), off Tone River mouth, Choshi, Chiba, 60 m, 21 Oct 1991, CBM-ZC 59; 2 ♂ (sl = 6.3, 10.7 mm), Hakodate Bay, 10–20 m, 17 Mar 1995, CBM-ZC 2362.

Diagnosis.—Gill lamellae biserial. Rostrum triangular. Maxillule with moderately well developed external lobe, not recurved. Right cheliped somewhat suboval in dorsal view; dorsal surface of palm weakly convex; dorsal surface of carpus with scattered spines mesiad of midline. Left cheliped with dorsal surface of palm weakly convex. Ambulatory legs similar; dactyls slightly longer than propodi, moderately slender, laterally compressed, in dorsal view slightly to prominently twisted, with longitudinal

sulcus on lateral face and row of corneous spines on ventral margin; carpi each with dorsodistal spine and row of low protuberances on dorsal surface. Fourth pereopods semichelate, preungual process apparently absent; propodal rasp with several rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subrectangular. Sternite of fifth pereopods (eighth thoracomere) separated into two somewhat flattened, rounded lobes by shallow median depression; coxae of fifth pereopods symmetrical. Males with papilla or very short sexual tube developed from coxa of both right and left fifth pereopods. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, biramous pleopods left on pleomeres 2–4; pleopod 5 reduced. Telson with posterior lobes separated by shallow median cleft; terminal margins broadly rounded, each unarmed or with few very small spinules adjacent to cleft.

Parapagurodes imaii (Yokoya, 1939)
Figs. 1G, 2G, H, 3G, 4I, 5H

Redescription by Komai (1994:33–38, figs. 1–3).

Supplemental material examined.—Japan: 1 ♂ (sl = 2.1 mm), 1 ovig. ♀ (sl = 1.6 mm), Funakoshi Bay, Iwate, Sanriku, 66 m, 25 May 1995, CM-ZC 1911; 1 ♂ (al = 2.5 mm), off Takeoka, Boso Peninsula, ca 80 m, 2 Mar 1995, CBM-ZC 2699.

Diagnosis.—Gill lamellae biserial, but with slight terminal concavity, cleft or depression. Rostrum triangular. Maxillule with moderately well developed external lobe, not recurved. Right cheliped elongate in large males, dorsal surface of palm convex; dorsal surface of carpus with two longitudinal rows of spines. Left cheliped with dorsal surface of palm elevated in midline. Ambulatory legs somewhat dissimilar, third sexually dimorphic; dactyls of second and third right slightly shorter to slightly longer than propodi, moderately slender, laterally compressed, in dorsal view barely twisted, with row of corneous spines on ventral margin, third left of females broadened, propodus with prominent ventral spine; carpi each with dorsodistal spine and row of low, sometimes spinulose protuberances on dorsal surface. Fourth pereopods semichelate; preungual process absent; propodal rasp with 2 or 3 rows of corneous scales. Sternite of third pereopods (sixth thoracomere) subcircular to subovate, slightly skewed. Sternite of fifth pereopods (eighth thoracomere) separated into two somewhat flattened, rounded lobes by shallow median depression; coxae of fifth pereopods symmetrical. Males with very short sexual tube developed from coxa of both right and left fifth pereopods. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, biramous left pleopods on pleomeres 2–4; pleopod 5 reduced. Telson with posterior lobes separated by shallow median cleft; terminal margins oblique, each with 3 or 4 moderate to strong spines.

Parapagurodes doederleini (Doflein, 1902)
Figs. 1H, 2I, J, 3H, 4J, 5I

Redescription by Asakura (2001:885–888, figs. 45–47).

Supplemental material examined.—Japan: 2 ♂ (sl = 8.1, 9.2 mm), off Kochi, Tosa Bay, 190 m, 10 Aug 1991, CBM-ZC 184.

Taiwan: 1 ♂ (sl = 9.3 mm), 1 ♀ (sl = 7.8 mm), Su-Aou, 100–200 m, 6 Aug 1996, CBM-ZC 2922.

Diagnosis.—Gill lamellae biserial. Rostrum triangular. Maxillule with moderately well developed endopodal external lobe, not recurved. Right cheliped stout, dorsal surface of palm slightly convex; dorsal surface of carpus with covering of spines and spinulose tubercles. Left cheliped with dorsal surface of palm very slightly elevated in midline. Ambulatory legs dissimilar, dac-

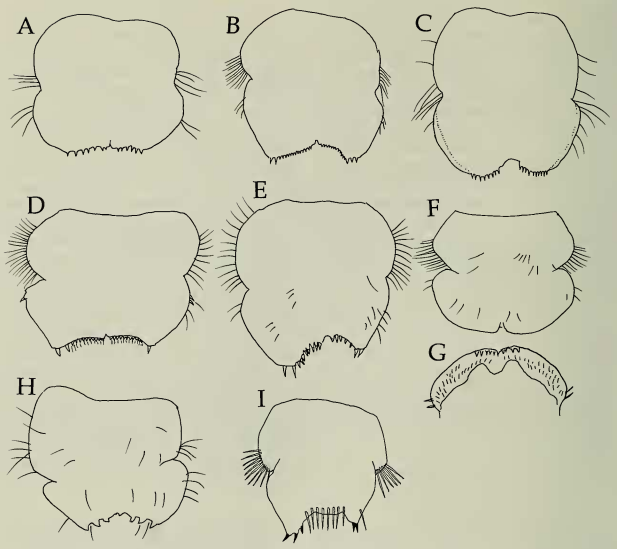

Fig. 5. Telson (A–F, H, I, dorsal view, G, ventral view of posterior portion). A, *Parapagurodes makarovi* McLaughlin & Haig, 1973 ♂ (sl = 3.5 mm), LACM; B, *P. laurentae* McLaughlin & Haig, 1973, ♂ (sl = 3.4 mm), LACM; C, *P. hartae* McLaughlin & Jensen, 1996, ♂ (sl = 3.2 mm), RBCPM 974-00368-22; D, *P. gracilipes* (Stimpson, 1858), ♂ (sl = 9.0 mm), CBM-ZC 2977; E, *P. nipponensis* (Yokoya, 1933), ♂ (sl = 7.3 mm), CBM-ZC 1162; F, G, *P. constans* (Stimpson, 1858); ♂ (sl = 8.7 mm), CBM-ZC 59; H, *P. imaii* (Yokoya, 1939), ♂ (sl = 2.5 mm), CBM-ZC 2699; I, *P. doederleini* (Doflein, 1902), ♂ (sl = 8.6 mm), ZSSM 274/1. A, B redrawn from McLaughlin & Haig (1973); C redrawn from McLaughlin & Jensen (1996); I from Asakura (2001).

tyls longer than propodi, strongly twisted, second left with row of 40–60 well developed, comb-like corneous spines on ventral margin; second right and third each with longitudinal row of short transverse rows of setae; carpi each with row of spines on dorsal surface. Fourth pereopods subchelate; preungual process absent; propodal rasp with 3 or 4 rows of corneous scales. Sternite of third pereopods (sixth thoracomere) rectangular. Sternite of fifth pereopods (eighth thoracomere) as narrow rod with pair of rounded lobes anteriorly; coxae of fifth pereopods asymmetrical. Males with very short sexual tube developed from coxa of right fifth pereopod, left sometimes with papilla. No paired pleopods in either sex. Males with unequally biramous left pleopods on pleomeres 3–5. Females with moderately well developed, biramous left pleopods on pleomeres 2–4; pleopod 5 reduced. Telson with posterior lobes separated by

broad, deep median concavity; terminal margins oblique, each with 1–5 moderate to strong corneous spines.

Results

In her discussion of significant generic characters, de Saint Laurent-Dechancé (1966) listed three that are pertinent to our investigation: sexual tube development, development of the external lobe of the maxillulary endopod, and pleopod number and development. Perusal of the abbreviated diagnoses of the eight species currently assigned to *Parapagurodes* shows that attributes of these three characters are not universally shared.

While sexual tube length (Fig. 1) varies from very short to short in *P. makarovi* (Figs. 1A, B) and *P. laurentae* (Fig. 1C, D) only very short tubes develop in the other six species (Figs. 1E–J), and occasionally are not apparent at all. However, recent studies have shown that sexual tube development is known to vary within genera (e.g., McLaughlin 1997, 2003; McLaughlin & Lemaitre 2001; Lemaitre & McLaughlin 2003a, 2003b). Nevertheless, *P. doederleini* is more importantly distinguished from the other seven species because in addition to the very short right sexual tube, the coxae of the male fifth pereopods are asymmetrical (Fig. 1J).

The external lobe of the maxillulary endopod (Fig. 2) is moderately well developed in all eight species, but is slightly to distinctly recurved only in *P. gracilipes* and *P. nipponensis* (Figs. 2D, E).

Parapagurodes was initially characterized as having unpaired male pleopods varying from reduced on pleomeres 3–5 to completely absent, and female unpaired pleopods often being reduced on pleomeres 2–4 and absent on pleomere 5. All subsequently assigned taxa are described as having at least moderately well developed unpaired, unequally biramous pleopods on male pleomeres 3–5 and on female pleomeres 2–5.

Several other characters frequently included in generic diagnoses also have been examined. Rostral development, for example is generally similar among species within a single genus. All eight species have an acutely developed rostrum, but then so do many species assigned to other genera.

With the exception of *P. constans,* all of the species under consideration herein are described as having an elongate right cheliped, at least in large males. In *P. hartae* and *P. imaii* this elongation is considered a sexually dimorphic character (McLaughlin & Jensen 1996, Komai 1999), whereas in *P. gracilipes* and *P. nipponensis* apparently the elongation is growth related (Komai 1998). Similar lengthening of the left cheliped is reported for these species. In contrast, the chelipeds are typically elongate regardless of sex or size in *P. makarovi, P. laurentae* and *P. doederleini.* That cheliped elongation is comparable among the eight taxa is doubtful.

Major differences among the eight species can be observed in the shape and armature of the dactyls of the ambulatory legs (Fig. 3). In *P. makarovi* and *P. laurentae* the dactyls (Figs. 3A, B) are moderately long, slender, laterally compressed, and in dorsal view appear straight; the dorsal surfaces of the carpi are armed only with a dorsodistal spine. The dactyls are similarly straight in *P. hartae* (Fig. 3C), but vary in length from shorter to only slightly longer than the propodi; the carpi each have a row of low protuberances on the dorsal surface in addition to the dorsodistal spine. The dactyls of *P. gracilipes* and *P. nipponensis* (Figs. 3D, E), although moderately long and laterally compressed, are moderate to broad and strongly twisted, the ventral margins of each are provided with a row of numerous small corneous spines; the dorsal surfaces of the carpi are provided with one or more rows of small spines. In contrast, while the dactyls of *P. constans* (Fig. 3F) are longer than the propodi and slightly to noticeably twisted, the ventral margins each are armed with fewer and much larger cor-

neous spines; each carpus is armed only with a row of low protuberances in addition to the dorsodistal spine. The dactyls of *P. imaii* and *P. doederleini* are dimorphic, but do not represent comparable conditions. As reported by Komai (1999), the third left dactyl and propodus of females of *P. imaii* differ from those of males. In males the dactyl and propodus of the third left (Fig. 3G) are moderately long and slender as they are on the second and third right. The female dactyl (Fig. 3H) is broad and prominently flattened; a well developed calcareous spine is present on the ventrodistal margin of the propodus. The dimorphism in *P. doederleini* involves the dactyls of the second pereopods. The left is provided with a ventral row of closely-spaced, corneous spines that present a comb-like appearance (Fig. 3I); the right, and the dactyls of the third pereopods completely lack spines, and instead are provided with short transverse rows of setae over the entire length of the mesial faces (Fig. 3J).

The shape of the anterior lobe of the sternite of the third pereopods and the configuration of the sternite of the fifth pereopods have been proposed as generic or at least group characters (e.g., McLaughlin 1981, 2003; Lemaitre et al. 1982). The anterior lobe of the sternite of the third pereopods is subsemicircular in *P. makarovi, P. laurentae,* and *P. hartae,* semicircular or subovate in *P. imaii,* but subquadrate to subrectangular in *P. gracilipes* and *P. nipponensis* and subrectangular in *P. constans* and *P. doederleini.* The sternites of the fifth pereopods are less clearly definable in these eight taxa.

The fourth pereopods (Fig. 4) are subchelate or only very weakly semichelate in *P. makarovi* and *P. laurentae* and *P. doederleini,* but semichelate in the remaining species. The number of rows of corneous scales making up the propodal rasps of these appendages exhibit overlapping intraspecific variation in all eight species.

The telsons of *P. makarovi* and *P. laurentae* (Figs. 5A, B) have straight to weakly concave or very slightly oblique terminal margins that are armed with small spines or spinules. Similar conformation and armature are seen in *P. gracilipes* (Fig. 5D) and to a lesser extent in *P. nipponensis* (Fig. 5E). In contrast, the terminal margins of the telsons of *P. hartae* (Fig. 5C) and *P. constans* (Fig. 5F, G) are broadly rounded and unarmed or only weakly armed. The telson of *P. imaii* (Fig. 5H) differs in having distinctly oblique terminal margins, each armed with prominent spines, and the telson of *P. doederleini* (Fig. 5I) is plainly different from the other seven.

Conclusions

From the evidence presented, there can be little doubt that *Parapagurodes,* as presently constituted, represents a heterogeneous collection of taxa. Consequently, we restrict *Parapagurodes* to the two species initially assigned, *P. makarovi* and *P. laurentae. Parapagurodes hartae* is herein transferred to *Pagurus* and the four species formerly included in *Pagurus* are returned to it.

We concur with Komai (1998) that *P. gracilipes* and *P. nipponensis* are closely allied to the *bernhardus* group of *Pagurus,* and undoubtedly should be included in that group. We do not advocate separating the *bernhardus* group from the admittedly polyphyletic *Pagurus* at this time, as *Pagurus bernhardus* (Linnaeus, 1758) is the type species of the genus. To remove *P. bernhardus* and its allied species would leave the remaining 80 or so species without generic union. Consequently, until such time as all species currently assigned to *Pagurus* have been thoroughly recognized and defined, this genus necessarily must remain a "catch-all". In contrast, there is ample justification to establish a new genus for the very distinctive *P. doederleini* as is done herein.

Dofleinia gen. nov.

Catapagurus: Doflein 1902:624 (in part).—Miyake 1978:78 (key, in part), 141 (in

part); 1982:232 (key, in part); 1991:232 (key, in part); 1999:232 (key, in part).

Parapagurodes: Asakura 2001:885 (in part).

Diagnosis.—Gills biserial; 11 pairs. Rostrum well developed, acute. Antennal peduncles with supernumerary segmentation. Maxillule with external lobe of endopod moderately well developed, not recurved. Third maxilliped with well developed crista dentata, 1 accessory tooth. Sternite of third maxillipeds unarmed. Chelipeds subequal, right stronger but not necessarily longer. Second pereopods dimorphic, left with row of closely-spaced comb-like corneous teeth on ventral margin, right with ventral margin unarmed. Third pereopods similar; sternite with subrectangular anterior lobe. Fourth pereopods subchelate; dactyl with well developed preungual process; propodal rasp consisting of 3 or 4 rows of corneous scales. Fifth pereopods chelate; coxae of males asymmetrical. Males with very short sexual tube developed from right gonopore, papilla frequently produced from left.

Abdomen well developed, twisted; columellar muscle usually prominent. Males without paired first or second pleopods; with unequally biramous unpaired left pleopods 3–5. Females without paired first pleopods, with subequally biramous, unpaired, left pleopods 2–4, pleopod 5 as in male. Uropods asymmetrical. Telson with distinct lateral indentations; posterior lobes separated by very broad median cleft.

Type species.—*Catapagurus doederleini* Doflein, 1902.

Etymology.—Named after F. Doflein who first described the type species; gender feminine.

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Literature Cited

Asakura, A. 2001. A revision of the hermit crabs of the genera *Catapagurus* A. Milne-Edwards and *Hemipagurus* Smith from the Indo-West Pacific (Crustacea: Decapoda: Anomura: Paguridae).—Invertebrate Taxonomy 15:823–891.

Doflein, F. 1902. Ostasiatische Dekapoden.—Abhandlungen der Kgl. Bayerischen Akademie der Wissenschaften Math.-Phys. Klassen. 21:613–670.

Hart, J. F. L. 1982. Crabs and their relatives of British Columbia.—British Columbia Provincial Museum Handbook 40:1–266.

Henderson, J. R. 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–76. Scientific Results of the Exploratory Voyage of HMS Challenger, (Zoology) 27:1–221. Her Majesty's Stationary Office, Edinburgh etc.

Jensen, G. C. 1995. Pacific coast crabs and shrimps. viii + 87 pp. Sea Challengers, Monterey, CA.

Komai, T. 1994. Rediscovery of *Pagurus imaii* (Yokoya, 1939) (Decapoda Anomura: Paguridae) from Hokkaido, Japan.—Natural History Research, 3(1):33–39.

———. 1998. The taxonomic position of *Pagurus gracilipes* (Stimpson, 1858) and *Pagurus nipponensis* (Yokoya, 1933), and description of a new species of *Pagurus* (Decapoda, Anomura, Paguridae) from Japan.—Zoosystema 20:265–288.

———. 1999. Reexamination of the type material of *Pagurus sagamiensis* Miyake (Decapoda: Anomura: Paguridae).—Natural History Research 5(2):79–92.

Lemaitre, R., P. A. McLaughlin, & J. García-Gómez. 1982. The *Provenzanoi* group of hermit crabs (Crustacea, Decapoda, Paguridae) in the Western Atlantic, part IV. A review of the group, with notes on variations and abnormalities.—Bulletin of Marine Science 32:670–701.

———, & ———. 2003a. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae) with descriptions of new genera and species. Addendum and taxonomic summary.—Proceedings of the Biological Society of Washington 116:464–486.

———, & ———. 2003b. New species of the genus *Goreopagurus* (Decapoda: Anomura: Paguridae) from Tasmania and reevaluation of sexual tubes in hermit crab systematics.—Memoirs of Museum Victoria 60:221–227.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species Cum Characteribus, Differentiis, Synonymis, Locis, edition 10. 1, pp. i–iii, 1–824. Holmiae.

McLaughlin, P. A. 1974. The hermit crabs (Crustacea Decapoda, Paguridea) of northwestern North America.—Zoologische Verhandelingen 130:1–396.

———. 1981. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: part I. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne-Edwards and Bouvier.—Bulletin of Marine Science 31:1–30.

———. 1997. Crustacea Decapoda: hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. *In* A. Crosnier & P. Bouchet, eds., Résultats des Campagnes MUSORSTOM, 16.—Mémoires du Muséum national d'Histoire naturelle 172:433–572.

———. 2003. Illustrated keys to the families and genera of the superfamily Paguroidea (Crustacea: Decapoda; Anomura), with supplemental diagnoses of the genera of the Paguridae.—Memoirs of Museum Victoria 60:111–144.

———, & J. Haig. 1973. On the status of *Pagurus mertensii* Brandt, with descriptions of a new genus and two new species from California (Crustacea: Decapoda: Paguridae).—Bulletin of the Southern California Academy of Sciences 72: 113–136.

———, & G. S. Jensen. 1996. A new hermit crab species of the genus *Parapagurodes* from the eastern Pacific, with a description of its first zoeal stage.—Journal of Natural History 30: 841–854.

———, & R. Lemaitre. 2001. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species, part VI. *Pylopagurus* Milne-Edwards and Bouvier, *Haigia* McLaughlin, and *Pylopaguridium* new genus.—Proceedings of the Biological Society of Washington 114:444–483.

Milne-Edwards, A. 1880. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey steamer "Blake", Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les Crustacés.—Bulletin of the Museum of Comparative Zoology, Harvard College, 8(1):1–68.

Miyake, S. 1978. The crustacean Anomura of Sagami Bay: 1–200 (English), 1–161 (Japanese), Biological Laboratory, Imperial Household, Tokyo.

———. 1982. Japanese crustacean decapods and stomatopods in color, vol. 1. Macrura, Anomura and Stomatopoda. 261 pp. Hoikusha Publishing Co., Osaka (in Japanese).

———. 1991. Japanese crustacean decapods and stomatopods in color, vol. 1. Macrura, Anomura and Stomatopoda. Second printing. 261 pp. Hoikusha Publishing Co., Osaka (in Japanese).

———. 1999. Japanese crustacean decapods and stomatopods in color, vol. 1. Macrura, Anomura and Stomatopoda. Third printing. 261 pp. Hoikusha Publishing Co., Osaka (in Japanese).

Saint Laurent-Dechancé, M. de. 1966. Remarques sur la classification de la famille des Paguridae et sur la position systématique d'*Iridopagurus* de Saint Laurent. Diagnose d'*Anapagrides* gen. nov.—Bulletin du Muséum national d'Histoire naturelle (2)38:257–265.

Saint Laurent, M. de. 1969. Révision des genres *Catapaguroides* et *Cestopagurus* et description de quatre genres nouveaux. III. *Acanthopagurus* de Saint Laurent (Crustacés Décapodes Paguridae).—Bulletin du Muséum national d'Histoire naturelle (2)41:731–741.

Schram, F. R., & S. Koenemann. 2003. Developmental genetics and arthropod evolution: on body regions of crustaceans.—Crustacean Issues 15: 75–92.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federate missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. VII. [Preprint (December 1858) from] Proceedings of the Academy of Natural Sciences of Philadelphia 1858 [1859]:225–252.

Yokoya, Y. 1933. On the distribution of decapod Crustacea inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. "Soyo Maru" during the years 1923–1930.—Journal of the College of Agriculture Tokyo Imperial University 12:1–236.

———. 1939. Macrura and Anomura of decapod Crustacea found in the neighbourhood of Onagawa, Miyagi-ken.—Scientific Reports of Tohoku University 14:261–289.